The southernmost occurrence of the aquatic sloth thalassocnus (Mammalia, Tardigrada) in two new pliocene localities in Chile

De Los Arcos, Saleta ; Partarrieu, Diego ; Carrillo-Briceño, Jorge ; Amson, Eli

Abstract: Thalassocnus is a sloth (Mammalia, Tardigrada) adapted to an aquatic lifestyle. It was first described from the Neogene deposits of the Pisco Formation of Peru, from where most of the specimens come. The genus is represented by five species ranging from the late Miocene to the late Pliocene, occupying successive stratigraphic levels. Morpho-functional studies of the cranial and postcranial skeleton of Thalassocnus have demonstrated the progressive adaptation of these sloths to a marine environment, establishing gradual differences from from the geologically oldest to the youngest species of the genus. The first records of Thalassocnus outside the Pisco Formation have been referred to the Neogene Bahía Inglesa Formation, in northern Chile, where older species were recovered. In this paper, we describe materials from two new Pliocene localities in Chile: the Coquimbo and the Horcón formations, in northern and central Chile, respectively. The Coquimbo Formation material was collected from the Lomas del Sauce locality and consists of a partial skeleton of a single individual. Detailed comparisons of the elements with diagnostic features enabled the referral of this specimen to T. carolomartini. The material from the Horcón Formation was collected from the Playa La Luna locality and consists of an isolated phalanx, which is attributed to one of the species of Thalassocnus younger than T. natans. Thus, we present the first record of younger species of Thalassocnus in Chile and the southernmost occurrence of the genus. Key words. Coquimbo Formation. Horcón Formation. Marine assemblage. Tardigrada. Thalassocnus. Xenarthra. Resumen. EL HALLAZGO MÁS MERIDIONAL DEL PEREZOSO MARINO THALASSOCNUS (MAMMALIA, TARDIGRADA) EN DOS NUEVAS LOCALIDADES DEL PLIOCENO DE CHILE. Thalassocnus es un perezoso (Mammalia, Tardigrada) adaptado al medio acuático que fue descrito por primera vez en depósitos neógenos de la Formación Pisco en Perú, de la cual procede la mayor parte de los especímenes conocidos. El género está representado por cinco especies, que se extienden desde el Mioceno tardío al Plioceno tardío, ocupando niveles estratigráficos sucesivos. Estudios morfo-funcionales del esqueleto craneal y postcraneal de Thalassocnus han permitido constatar la progresiva adaptación de este perezoso al medio acuático, desde las especies geológicamente más antiguas a las más recientes. Los primeros registros de Thalassocnus fuera de la Formación Pisco corresponden a la Formación Bahía Inglesa, del Neógeno del Norte de Chile, y fueron asignados a las especies antiguas. En este trabajo describimos material de Thalassocnus procedente de dos nuevas localidades en depósitos pliocenos de las formaciones Coquimbo y Horcón, del Norte y Centro de Chile respectivamente. El material de la Formación Coquimbo proviene de la localidad Lomas del Sauce y pertenece a un único individuo que conserva buena parte del esqueleto postcraneal. La comparación detallada de aquellos elementos óseos con características diagnósticas ha permitido asignarlo a T. carolomartini. El material de la Formación Horcón, colectado en la localidad Playa La Luna, es una falange aislada, que fue asignada a alguna de las especies más recientes que T. natans. Se muestran por tanto los registros más meridionales de Thalassocnus y los primeros de las especies recientes en Chile. Palabras clave. Formación Coquimbo. Formación Horcón. Ensamble marino. Tardigrada. Thalassocnus. Xenarthra.

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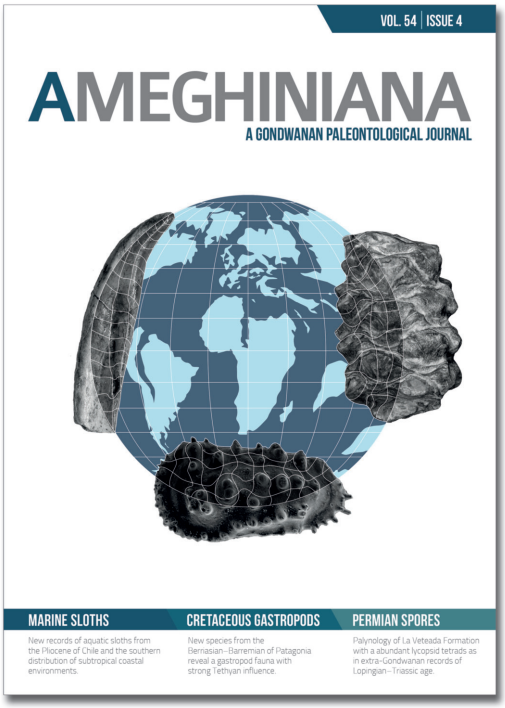

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THE SOUTHERNMOST OCCURRENCE OF THE AQUATIC SLOTH *THALASSOCNUS* (MAMMALIA, TARDIGRADA) IN TWO NEW PLIOCENE LOCALITIES IN CHILE

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Abstract. *Thalassocnus* is a sloth (Mammalia, Tardigrada) adapted to an aquatic lifestyle. It was first described from the Neogene deposits of the Pisco Formation of Peru, from where most of the specimens come. The genus is represented by five species ranging from the late Miocene to the late Pliocene, occupying successive stratigraphic levels. Morpho-functional studies of the cranial and postcranial skeleton of *Thalassocnus* have demonstrated the progressive adaptation of these sloths to a marine environment, establishing gradual differences from from the geologically oldest to the youngest species of the genus. The first records of *Thalassocnus* outside the Pisco Formation have been referred to the Neogene Bahía Inglesa Formation, in northern Chile, where older species were recovered. In this paper, we describe materials from two new Pliocene localities in Chile: the Coquimbo and the Horcón formations, in northern and central Chile, respectively. The Coquimbo Formation material was collected from the Lomas del Sauce locality and consists of a partial skeleton of a single individual. Detailed comparisons of the elements with diagnostic features enabled the referral of this specimen to *T. carolomartini*. The material from the Horcón Formation was collected from the Playa La Luna locality and consists of an isolated phalanx, which is attributed to one of the species of *Thalassocnus* younger than *T. natans*. Thus, we present the first record of younger species of *Thalassocnus* in Chile and the southernmost occurrence of the genus.

Key words. Coquimbo Formation. Horcón Formation. Marine assemblage. Tardigrada. *Thalassocnus*. Xenarthra.

Resumen. EL HALLAZGO MÁS MERIDIONAL DEL PEREZOSO MARINO *THALASSOCNUS* (MAMMALIA, TARDIGRADA) EN DOS NUEVAS LOCALIDADES DEL PLIOCENO DE CHILE**.** *Thalassocnus* es un perezoso (Mammalia, Tardigrada) adaptado al medio acuático que fue descrito por primera vez en depósitos neógenos de la Formación Pisco en Perú, de la cual procede la mayor parte de los especímenes conocidos. El género está representado por cinco especies, que se extienden desde el Mioceno tardío al Plioceno tardío, ocupando niveles estratigráficos sucesivos. Estudios morfo-funcionales del esqueleto craneal y postcraneal de *Thalassocnus* han permitido constatar la progresiva adaptación de este perezoso al medio acuático, desde las especies geológicamente más antiguas a las más recientes. Los primeros registros de *Thalassocnus* fuera de la Formación Pisco corresponden a la Formación Bahía Inglesa, del Neógeno del Norte de Chile, y fueron asignados a las especies antiguas. En este trabajo describimos material de *Thalassocnus* procedente de dos nuevas localidades en depósitos pliocenos de las formaciones Coquimbo y Horcón, del Norte y Centro de Chile respectivamente. El material de la Formación Coquimbo proviene de la localidad Lomas del Sauce y pertenece a un único individuo que conserva buena parte del esqueleto postcraneal. La comparación detallada de aquellos elementos óseos con características diagnósticas ha permitido asignarlo a *T. carolomartini*. El material de la Formación Horcón, colectado en la localidad Playa La Luna, es una falange aislada, que fue asignada a alguna de las especies más recientes que *T. natans*. Se muestran por tanto los registros más meridionales de *Thalassocnus* y los primeros de las especies recientes en Chile.

Palabras clave. Formación Coquimbo. Formación Horcón. Ensamble marino. Tardigrada. *Thalassocnus*. Xenarthra.

Thalassocnus Muizon and McDonald, 1995 is an aquatic sloth (Mammalia, Tardigrada) that was first described in the Neogene Pisco Formation of Peru (Muizon and McDonald, 1995). This formation contains a diverse fauna, typical of a littoral environment, that includes molluscs, brachiopods, crustaceans, teleosteans, selachians, sea birds, cetaceans, and pinnipeds (Bianucci *et al.*, 2016, and references therein). The genus *Thalassocnus* consists of five species initially described based on the skull, mandible, dentition, and a few postcranial elements (Muizon and McDonald, 1995;

McDonald and Muizon, 2002; Muizon *et al.*, 2003, 2004a) with a temporal range that spans from the late Miocene to the late Pliocene (Muizon *et al.*, 2003, 2004a; Amson *et al.*, 2015b). The five species were found in five successive stratigraphic levels that were dated using absolute methods (Muizon and DeVries, 1985; Muizon *et al.*, 2004a; Ehret *et al.*, 2012): *Thalassocnus antiquus* Muizon, McDonald, Salas, and Urbina, 2003, located in the Aguada de Lomas horizon (AGL) that ranges in age from 8 to 8.8 Ma (Huayquerian SALMA); *Thalassocnus natans* Muizon and McDonald, 1995, found in the Montemar horizon (MTM), dated to 7.30 Ma (Huayquerian SALMA); *Thalassocnus littoralis* McDonald and Muizon, 2002, located in several levels of the Sacaco Sur horizon (SAS), dated from 7.1 Ma to 5.93 Ma (late Huayquerian to late Montehermosan SALMA); and *Thalassocnus carolomartini* McDonald and Muizon, 2002, found at the Sacaco horizon with an age of 5.75 Ma (Montehermosan SALMA). No absolute dating exists for the deposits where the *Thalassocnus yaucensis* Muizon, McDonald, Salas, and Urbina 2004 material is present; however, a stratigraphic correlation enables the estimation of a Pliocene or early Pliocene age.

The first reconstruction of the aquatic lifestyle of *Thalassocnus* was made on the basis of taphonomic arguments and a few anatomical features (Muizon and McDonald, 1995). Subsequent studies analyzing the functional morphology of the skeleton and bone microstructure revealed a gradual adaptation to a marine environment from the oldest to the youngest species of *Thalassocnus*. Different feeding adaptations were demonstrated based on cranial, mandibular and dental characters, and enabled the recognition of the three oldest species as partial grazers (most likely of stranded or shallow marine vegetation), and the two youngest species as specialized grazers (Muizon *et al.*, 2004b). Gradual increases in bone compactness (osteosclerosis) and volume (pachyostosis) were observed from the oldest to the youngest species, affecting both the ribs and long bones (Amson *et al.*, 2015a). Such modifications would facilitate buoyancy control and stability in aquatic environments. Forelimb and hind limb morphology also support gradual adaptation to an aquatic lifestyle (Amson *et al.*, 2015b, c), suggesting that aquatic locomotion was achieved by means of "quadrupedal paddling" and "bottom walking". Manus morphology showed the capability for gripping fixed objects on the seafloor, which may have facilitated *Thalassocnus* feeding and stabilization (Amson *et al.*, 2015b); moreover, secondary plantigrady in the youngest species, and the development of a strong claw on the third digit of the pes would also have favored this stabilization (Amson *et al.*, 2015c). Forelimb adaptations are also consistent with digging habits (Amson *et al.*, 2015b). Axial postcranium morphology of the youngest species showed adaptations consistent with a greater amount of time spent in water and a downturned inclination of the head, constituting an adaptation to grazing on the sea floor (Amson *et al.*, 2015d). Furthermore, the genus is characterized by a long tail that would have enabled the stabilization of the body while feeding.

Most of the specimens of *Thalassocnus*, including the most complete remains, come from the Pisco Formation, but additional findings in Neogene marine deposits from Chile, in the Bahía Inglesa Formation, had already been reported (Canto *et al.*, 2002, 2008; Walsh and Suárez, 2005; Suárez *et al.*, 2011; Pyenson *et al.*, 2014). The first report of *Thalassocnus* from Chile corresponded to a partial mandible found in the Miembro Lechero of the Bahía Inglesa Formation (Canto *et al.*, 2002). The material (SGO.PV1093) was referred to *T. antiquus* or *T. natans* (Canto *et al.*, 2008), consistent with the assignment of the deposits to the late Miocene, as indicated by radiometric ages derived from ash levels in the formation.

Subsequent findings of *Thalassocnus* in deposits of the Bahía Inglesa Formation were reported by Suárez *et al.* (2011). In the locality "Arenas de Caldera", attributed to the late Miocene (Walsh and Suárez, 2005), two femora were preliminary assigned to *Thalassocnus* sp. (SGO.PV 1133). The specimens housed in the Museo Paleontológico de Caldera (MPC-SPN2) comprise some elements of the postcranial skeleton and a cranium, and were attributed to *T. natans,* except for a specimen with characteristics intermediate between *T. natans* and *T. littoralis*.

Thanks to the 2010 to 2012 road expansion of the Pan-American Highway at the Cerro Ballena locality in Caldera, new isolated remains attributed to *T. natans* from the Bahía Inglesa Formation were recovered (Pyenson *et al.*, 2014). This attribution allowed these authors to assign the upper boundary of the section to the late Miocene on the basis of the correlation with the Montemar horizon of the Pisco For-

mation. Although initially based on characters shared by the entire genus, this attribution was subsequently confirmed (Amson *et al.*, 2015c): the morphology of the medial trochlear ridge of the femur enabled the attribution of the femur to either *T. antiquus* or *T. natans*. Thus, the upper age limit of the Cerro Ballena site might be as initially supposed or older (Amson *et al.*, 2015c).

In this work, we present new material of *Thalassocnus* from the Neogene Coquimbo and Horcón formations, located in north and central Chile, respectively (Fig. 1). The Coquimbo material comes from the new locality Lomas del Sauce and consists of a partial skeleton of a single individual recovered during a systematic excavation in June 2015. The Horcón material ascribed to *Thalassocnus* is restricted to a single phalanx recovered in May 2011 by one of the authors (JCB) in level 12 of the upper member of the Horcón Formation (Carrillo-Briceño *et al.*, 2013).

GEOLOGICAL SETTING

The Pacific coastline of South America is marked by a series of Neogene basins that comprise marine deposits discontinuously exposed from Ecuador to Chile. Within these basins, several units, such as the Pisco, Bahía Inglesa, Coquimbo, and Horcón formations, are recognized (Fig. 1).

According to Martínez-Pardo (1979), after having been first studied by Darwin (1846), many of the Neogene marine deposits of northern-central Chile were referred to as "Coquimbo Formation", although often by an improper extension of the "Coquimbo Stufe" of Steinmann (1895). In view of this, Moscoso *et al.* (1982) proposed to reserve the term "Coquimbo Formation" for a set of marine sediments located along the coastline between 28° and 30° S. In La Herradura Bay area, the Formation appears as a succession of marine sediments including sandstones, siltstones, limestones, coquinas, and conglomerates, which have been attributed to the Pliocene-Pleistocene interval based on their fossil malacofauna (Herm, 1969; Emparan and Pineda, 2000). Different levels of marine terraces were carved in these sediments as a result of the Plio-Quaternary marine transgressions and regressions that occurred in this area (Paskoff, 1970; Paskoff *et al.*, 1995). The Lomas del Sauce locality is situated in the Herradura Bay sector (29° 59′ 42″ S; 71° 20′ 2″ W), where some of the higher levels of one of these terraces are recorded at an altitude of 60-70 m above

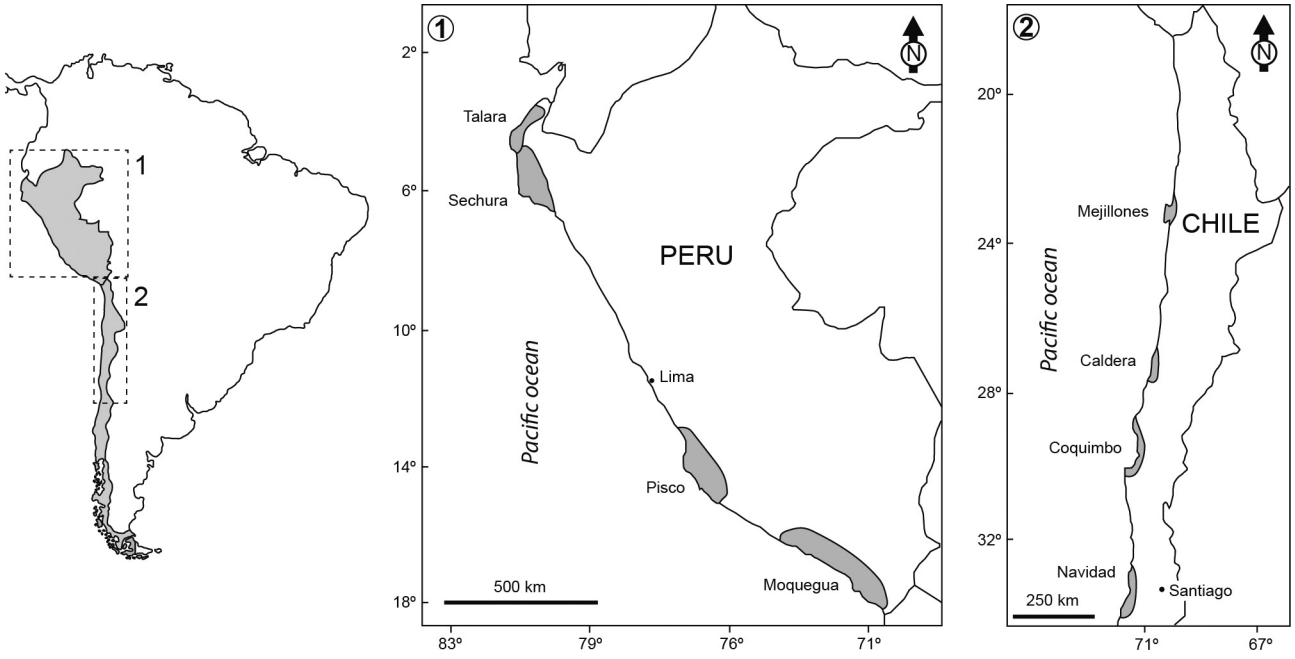

Figure 1. 1, Neogene sedimentary basins located along the Pacific coast of Peru and **2,** northern and central Chile. The Horcón Formation is part of the Navidad Basin , the Coquimbo Formation is included in the Coquimbo Basin and Bahía Inglesa Formation fills the Caldera Basin. Modified from Martínez-Pardo (1990).

sea level (Fig. 2). The stratigraphy of this locality is characterized by a succession of sandy to clayey poorly consolidated siltstones interbedded with two fossiliferous beds made up of silt and coquinas (Fig. 3) with abundant bivalve, gastropod, serpulid, barnacle, and decapod remains, as well as a conspicuous record of vertebrates including marine mammals, chondrichthyans, bony fishes, and birds. The fossil invertebrate assemblage in these levels enables their attribution to the Pliocene, taking into account the biostratigraphic ranges proposed by Guzmán *et al.* (2000) for the Caldera Formation. The presence of *Chorus grandis*, whose first occurrence dates from the early Pliocene (DeVries, 1997; Guzmán *et al.*, 2000), in combination with *Anadara chilensis*, characteristic of the Pliocene (upper and probably also to the early Pliocene), confirms this age assignement.

The *Thalassocnus* specimen from Lomas del Sauce was recovered from the upper fossiliferous bed (bed '3'), in the silt layer that underlies the serpulids crust (Fig. 3). Part of the axial postcranium, specifically the cervical and some thoracic vertebrae, and also the left humerus and scapula, were found articulated. The rest of the bones were dispersed in the area and isolated, although somewhat following the general body disposition. The pelvis was facing downwards whereas the axial postcranium and the forelimb remains were lying upwards, indicating that the postcranium suffered a slight displacement before burial. Some bones (pelvis, scapula, and humerus) were broken just before or during the burial, since broken fragments were lo-

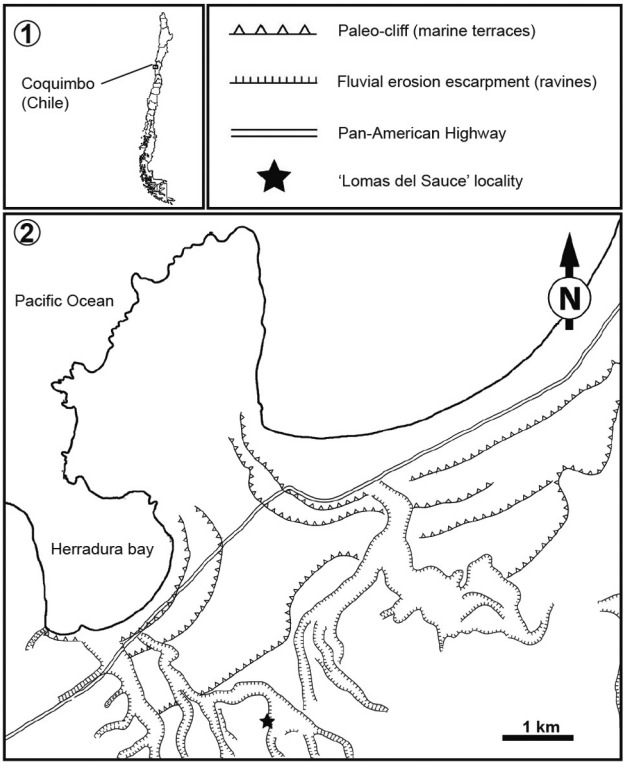

Figure 2. Map of fossiliferous locality of Lomas del Sauce. Modified from Paskoff *et al.* (1995).

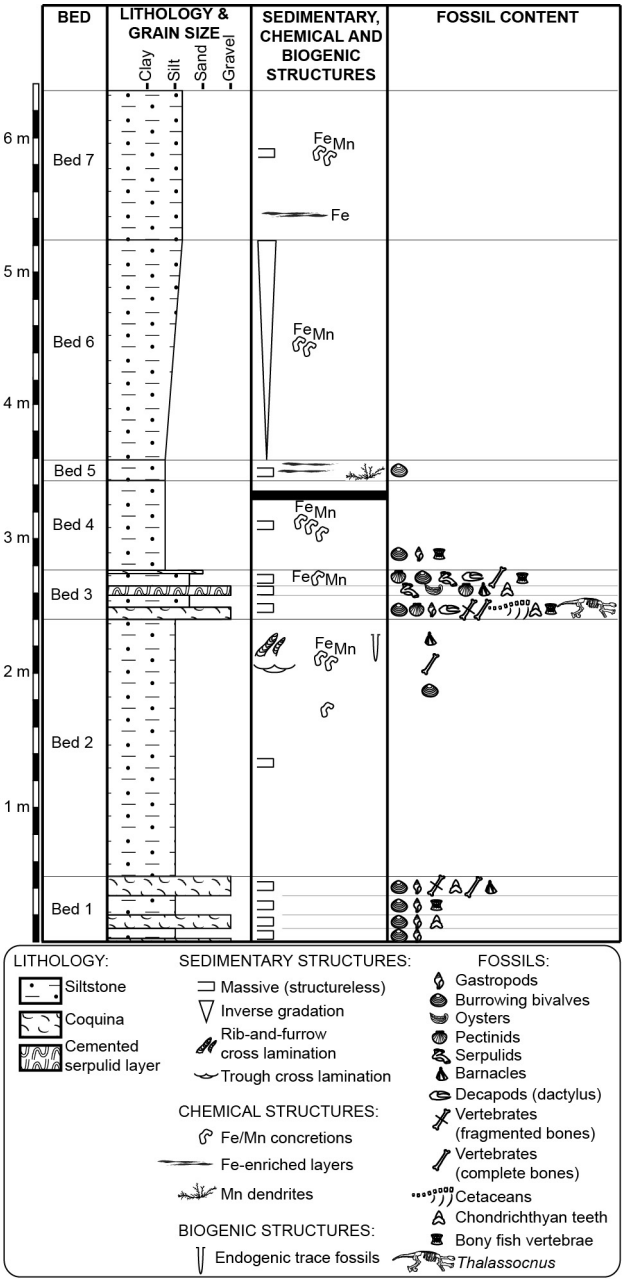

Figure 3. Stratigraphic column of the Lomas del Sauce locality.

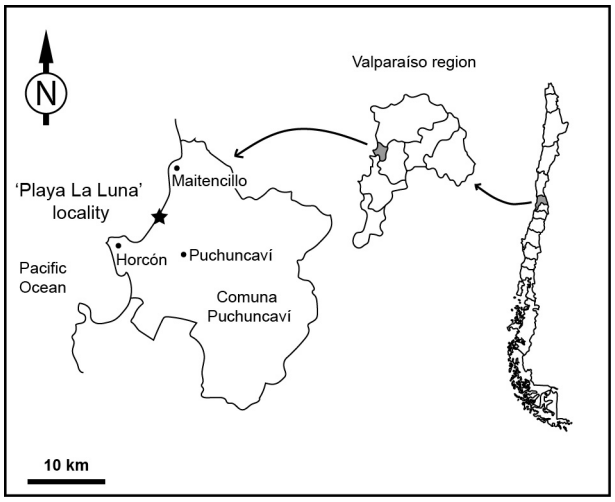

Figure 4. Map of fossiliferous locality Playa La Luna. Modified from Carrillo-Briceño *et al.* (2013).

cated *in situ*, showing only a slight vertical displacement. A phosphatic crust developed at the bottom of the fossiliferous level was fixed to most of the bones.

The Horcón Formation is part of the Neogene Navidad Basin and was defined by Thomas (1958) as a set of sediments that includes sandstones, mudstones, and siltstones forming a cliff along the coastline between Caleta Horcón and Maitencillo (Carrillo-Briceño *et al.*, 2013). Carrillo-Briceño *et al.* (2013) recognized two different stratigraphic intervals for this unit and assigned them to the upper interval of the Horcón Formation. According to Carrillo-Briceño *et al.* (2013), the lithology is dominated by fine to coarse sandstones poorly consolidated and interbedded with a few layers of conglomerates and boulders. Based on the association of fossil molluscs contained in these sequences, Carrillo-Briceño *et al.* (2013) proposed a late Pliocene age for the Horcón Formation. The phalanx described in this paper was collected in the Playa la Luna locality (32° 42′ 2″ S; 71° 27′ 38″ W), situated 3 km northeast of Caleta Horcón (Fig. 4). In this locality, a boulder bed overlies a medium-grained sandstone layer. The latter, which corresponds to layer '12' in Carrillo-Briceño *et al.* (2013), is a fossiliferous stratum where several remains of vertebrates have been found, such as sharks (Carrillo-Briceño *et al.*, 2013), bony fishes, birds (Chávez-Hoffmeister *et al.*, 2014), and some mammals currently under study.

MATERIAL AND METHODS

Both specimens described here are housed at the Museo Nacional de Historia Natural de Santiago (MNHN) in Chile. We will hereafter describe only the elements with specific diagnostic features.

Both specimens were compared with the previously recovered specimens ascribed to the five species of *Thalassocnus* using the descriptions of the postcranial skeleton provided by Amson *et al.* (2015b–d). Bone dimensions were measured following these authors (Tabs. 1–2). In order to refer to mediolateral, proximodistal, and anteroposterior directions of the long bones, the terms width, length, and depth were conventionally used. For the description and tables we used the following abbreviations: **AP,** anteroposterior; **D,** depth; **DP,** dorsopalmar; **DV,** dorsoventral; **L,** length; **LTR,** depth of the distal epiphysis at the level of the lateral trochlear ridge (femur); **ML,** mediolateral; **MTR,** anteroposterior depth of medial trochlear ridge at the level of the lateral trochlear ridge (femur); **PD,** proximodistal; **W,** width. Institutional abbreviations corresponds to: **SGO.PV,** Museo Nacional de Historia Natural, Santiago de Chile, Chile and **MUSM,** Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Perú.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
XENARTHRA Cope, 1889
TARDIGRADA Latham and Davies in Forster, 1795
(= PHYLLOPHAGA Owen, 1842; = FOLIVORA Delsuc, Catzeflis, Stanhope, Douzery, 2001)
MEGATHERIIDAE *sensu* Amson, Muizon, Gaudin, 2016
THALASSOCNINAE Muizon, McDonald, Salas, Urbina, 2004

Thalassocnus Muizon and McDonald, 1995
Thalassocnus carolomartini McDonald and Muizon, 2002
Figures 5–17

Referred specimen. SGO.PV 15500, partial postcranium comprising partial left scapula, right clavicle, complete left humerus, and distal end of right humerus, proximal end of right and distal end of left ulna, distal end of right radius, right scaphoid, almost complete digital complex of right manus, partial left and right femora, left and right patellae,

Table 1- Measurements of forelimb bones (in millimetres) of **T. carolomartini** *from Lomas del Sauce (SGO.PV 15500).*

Humerus	
Head, AP length	*58*
Head, ML width	*55*
Proximal tuberosity, greatest ML width	*94*
Radius	
Articular facet for manus, AP depth	*74*
Articular facet for manus, greatest ML width	*36*
ML width just proximal to distal epiphysis	*35*
Scaphoid	
Greatest PD length (at level of distal process)	*28*
Greatest ML width (at level of articular facet for MCC)	*53*
Greatest DP depth (at level of dorsal process)	*33*
ML width (W)	*53*
PD length (L)	*29*
W/L	*1.82*
Trapezium-first metacarpal complex	
Angle between facets with Mc II	*122*
Greatest PD length	*40*
Greatest ML width (at lateroproximal complex)	*34*
DP depth at midshaft	*19*
PD length (L)	*40*
DP depth (D)	*19*
L/D	*2.11*
Phalanx digit one	
Greatest PD length	*43*
Greatest ML width (at proximal end)	*25*
Greatest DP depth (at proximal end)	*34*
Metacarpal II	
Angle between the carina and vertical plane	*36*
Proximal phalanx, digit two	
Greatest PD length	*25*
Greatest ML width	*33*
Greatest DP depth	*36*
Middle phalanx, digit two	
Greatest PD length (at midwidth)	*49*
ML width at midshaft	*32*
DP depth at midshaft	*21*
Ungual phalanx, digit two	
Greatest PD length (N.B. the distal tip is rarely preserved)	*74.5*
PD length of subungual process	*42*
Greatest ML width (at proximal articular surface)	*33*
DP depth at proximal end	*30*
DP depth of ungual process palmar to level of subungual process	*15*
Digit three	
Angle between middle and ungual phalanxes when flexed	*61*
Proximal phalanx, digit three	
Greatest PD length	*23*
Greatest ML width	*30*
Greatest DP depth	*37*
Middle phalanx, digit three	
Greatest PD length (at midwidth)	*44*
ML width at midshaft	*26*
DP depth at midshaft	*18*
Ungual phalanx, digit three	
Greatest PD length	*97*
Greatest ML width (at proximal end)	*26*
Greatest DP depth (at proximal end)	*40*
Proximal phalanx, digit four	
Greatest PD length	*20*
Greatest ML width	*28*
Greatest DP depth	*38*
Middle phalanx, digit four	
Greatest PD length	*38*
Greatest ML width	*23*
Greatest DP depth (at proximal end)	*32*

Abbreviations: ***AP****, anteroposterior;* ***D****, depth;* ***DP****, dorsopalmar;* ***L****, length;* ***ML****, mediolateral;* ***PD****, proximodistal;* ***W****, width.*

partial left and right tibiae, and fibulae, right astragalus, left cuboid and fourth metatarsal, partial pelvis, cervical, some thoracolumbar and caudal vertebrae, and fragmentary ribs.

Locality and age. Lomas del Sauce locality, Coquimbo Formation, Pliocene.

Description. Based on the size of the femoral head, the Lomas del Sauce specimen is roughly 5% smaller than MUSM 434, the largest specimen of *Thalassocnus* known to date (referred to *T. yaucensis*, estimated to be *ca.* 330 cm long) (Amson *et al.*, 2015b, c). This would be consistent with the attribution to a younger species of *Thalassocnus*, as the largest body sizes are found in the younger (Amson *et al.*, 2015b,c).

The complete left humerus is preserved although par-

TABLE 2- Measurements of hind limb bones (in millimetres) of **T. carolomartini** *from Lomas del Sauce (SGO.PV 15500).*

Pelvis	
Ilium, maximum ML width of the iliac wing	*190**
Acetabulum, DV depth	*57*
Right femur	
Head, PD radius (normal to the base of the head, anterior view)	*43*
Head, ML diameter (normal to the base of the head)	*68*
Head, AP diameter (normal to the base of the head)	*66*
Proximal end, greatest ML width (from medial edge of head to lateral edge of greater trochanter)	*125*
Epicondyles, ML width (oblique to shaft)	*124*
MTR	*5.2*
LTR	*66.5*
MTR/LTR	*0.08*
Patella	
PD length of apex (La)	*25*
PD length of facet for femur at midwidth (Lf)	*34*
La/Lf	*0.73*
Tibia	
Greatest PD length	*272*
Proximal end, greatest ML width (at anterior tuberosity)	*29*
Proximal end, greatest AP depth	*48*
Distal end, greatest ML width	*42*
Astragalus	
Greatest PD length (at level of junction between medial and lateral trochleae)	*60*
Greatest ML width (between odontoid process and fibular facet)	*61*
Greatest DP depth (between dorsal edge of trochleae and level of plantar edge of navicular process)	*61*
Angle between trochleae in distal view (±5°)	*109*
Cuboid	
Greatest PD length	*36*
Greatest ML width	*32*
Greatest DP depth	*43*

*Abbreviations: *, approximate;* ***AP****, anteroposterior;* ***D****, depth;* ***DV****, dorsoventral;* ***L****, length;* ***LTR****, depth of the distal epiphysis at the level of the lateral trochlear ridge;* ***ML****, mediolateral;* ***MTR****, anteroposterior depth of medial trochlear ridge at the level of the lateral trochlear ridge;* ***W****, width.*

tially covered by a phosphatic crust on the anterior side that masks some features (Fig. 5). Older species of *Thalassocnus* present a shallow broad groove on the anterior surface of the lesser tuberosity at the proximal end of the humerus so it is subdivided into a larger medial process and a smaller process located on the lateral edge. In *T. carolomartini* and *T. yaucensis*, this groove is reduced. In the left humerus of the Lomas del Sauce specimen, this groove is absent. The transverse expansion of the distal end of the humerus is symmetric in the old species and asymmetric in *T. yaucensis* due to the reduction of the medial epicondyle. The Lomas del Sauce specimen shows a symmetrical distal epiphysis.

A partial proximal end of the right ulna and a distal end of the left ulna are preserved. The proximal end preserves only the portion at the level of the anconeal process so the articular facet for the humerus is partially preserved and the articular facet for the radius is not. The medial extension of

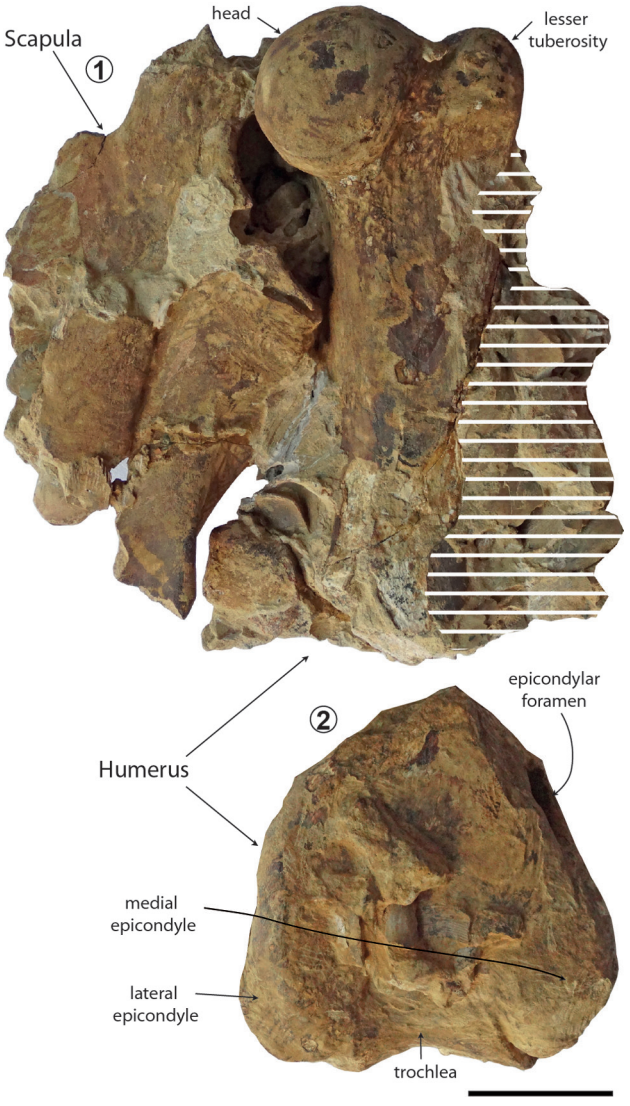

Figure 5. ***Thalassocnus carolomartini*** **(SGO.PV** 15500) from the Lomas del Sauce locality. **1,** left proximal humerus and partial left scapula in posterior view; **2,** left distal humerus in posterior view. Hatched area corresponds to the phosphatic crust with molluscs. Scale bar= 5 cm.

the posteromedial edge of the olecranon process is visible and reminiscent of the specimen of *T. carolomartini* figured by Amson *et al.* (2015b). The distal end has a well-developed surface for the articulation with the carpus, distally located and extending anteriorly. This surface is oval with its long axis extending anteromedially to posterolaterally. From the anteromedial edge of this facet, a small ridge departs to the medial edge of the bone, separating two small fossae. These fossae are not described in Amson *et al.* (2015b).

The distal end of the right radius is preserved (Fig. 6). The radius is one of the most clearly diagnostic elements in *Thalassocnus*. Interspecific variations are reflected in the radius length and the relative development of the pronator ridge, implying a progressive increase of the distal width from the oldest to the youngest species. Although fragmentary, the pronator ridge is clearly well developed in the Lomas del Sauce specimen, as it is in the younger species of the genus. Another diagnostic feature is found in the development of three prominent tendinal grooves on the lateral side of the distal radius. The central groove, for the extensor carpi radialis muscle, is wider and shallower in the younger species as well as more symmetrical anteroposteriorly. In the specimen of Lomas del Sauce, this groove is wide, shallow and anteroposteriorly symmetrical. Also on the posterior side of the distal epiphysis, the ulnar notch displays interspecific variations. This notch is almost absent in *T. natans* (no data for *T. antiquus*), shallow and well marked in *T. littoralis*, and extended well proximally in *T. carolomartini* and *T. yaucensis*. The ulnar notch is well defined and extends proximally in the Lomas del Sauce specimen. Another diagnostic character is the sulcus that extends from the central groove for the extensor carpi radialis muscle to the articular facet with the carpus. Species older than *T. carolomartini* possess this sulcus, which is reduced in *T. carolomartini* and absent in *T. yaucensis*. In the Lomas del Sauce specimen, this sulcus is present.

The complete right scaphoid is preserved (Fig. 7). The scaphoid of *T. carolomartini* is mediolaterally wider when compared to older species and even wider in *T. yaucensis*. Measurements of ML width and PD length in the scaphoid of the Lomas del Sauce specimen yield a ML/PD ratio of 1.82, which is between the mean values for *T. carolomartini* (1.72) and *T. yaucensis* (1.88) (Amson *et al.*, 2015b). The articular surface for the trapezium-Mc I complex and lunar are preserved in the Lomas del Sauce specimen. The latter completely occupies the lateral side of the bone and is a flat surface, a trait characteristic of *T. carolomartini* and *T. yaucensis* (it is clearly convex in *T. antiquus* and *T. natans*, and slightly convex in *T. littoralis*) (Amson *et al.*, 2015b). The articulation surface for the trapezoid is oval in the Lomas del Sauce specimen, not triangular as previously described for all species (Amson *et al.*, 2015b). Its long axis is oriented dorsopalmarly and extends along the dorsal and distal parts of the bone. This surface presents a convexity but is divided

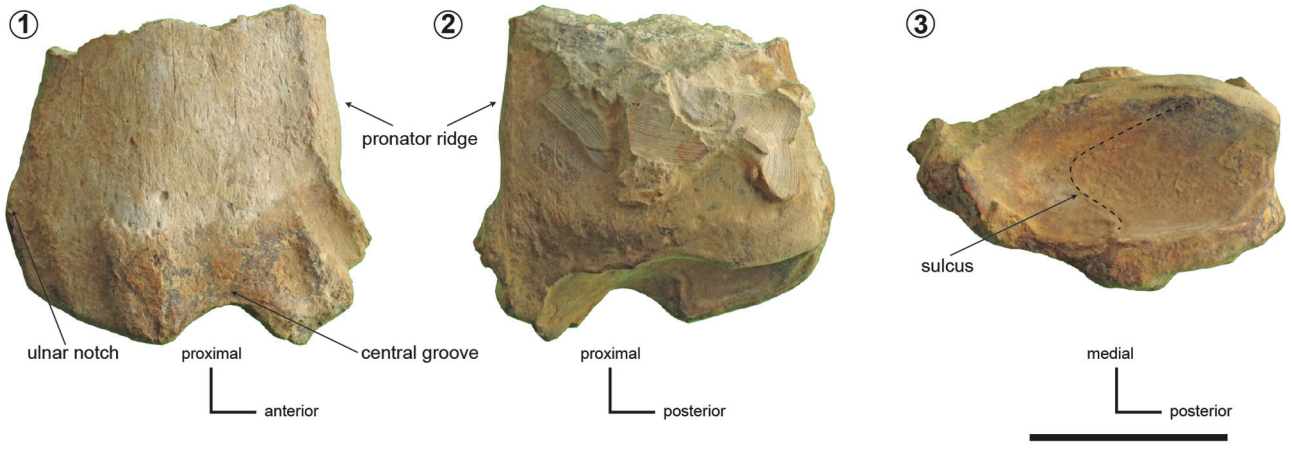

Figure 6. ***Thalassocnus carolomartini*** **(SGO.PV** 15500) from the Lomas del Sauce locality. Right radius distal end in: **1,** lateral view; **2,** medial view; **3,** distal view. Note the sulcus on the articular surface for carpus in distal view. Scale bar= 5 cm.

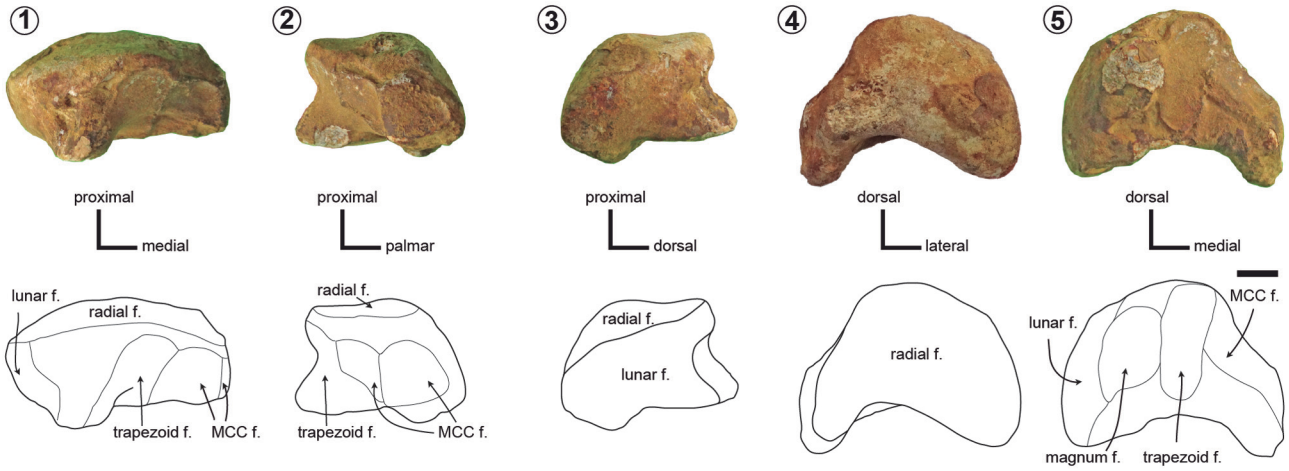

Figure 7. ***Thalassocnus carolomartini*** **(SGO.PV** 15500) from the Lomas del Sauce locality. Right scaphoid in: **1,** dorsal view; **2,** medial view; **3,** lateral view; **4,** proximal view; **5,** distal view. Abbreviation: **f,** facet; **MCC,** trapezium-first metacarpal complex. Scale bar= 1 cm.

into two shallow concavities separated by a shallow elevation. This description is consistent with that given for *T. yaucensis* (Amson *et al.*, 2015b). Another feature of the scaphoid of the Lomas del Sauce specimen shared with *T. carolomartini* and *T. yaucensis* is the absence of the distopalmar process. This process is well developed in *T. natans*, weaker in *T. littoralis*, and vestigial or absent in *T. carolomartini* and *T. yaucensis*.

The digital complex of the right manus is almost complete in the Lomas del Sauce specimen, lacking the third metacarpal, the ungual phalanx of digit four, and the phalanges of digit five (Fig. 8).

The first metacarpal in *Thalassocnus* is co-ossified with the trapezium forming the MCC complex, which is a short and stout bone (Amson *et al.*, 2015b). The ratio between its PD length and DP depth is 2.10 in the Lomas del Sauce specimen (see table 1), which is similar to the values in *T. carolomartini* and *T. yaucensis* but also to some of the values for *T. littoralis* (Amson *et al.*, 2015b). The articular surface for the second metacarpal in the Lomas del Sauce specimen extends along the lateral and palmar sides of the bone while the lateropalmar edge of the bone separates this surface into two almost flat facets. This description is consistent with that previously made for *T. antiquus* and *T. littoralis* (Amson *et al.*, 2015b) because, in *T. carolomartini* (no data for *T. yaucensis*), both facets are slightly convex.

The proximal and ungual phalanges of digit one in *Thalas-*

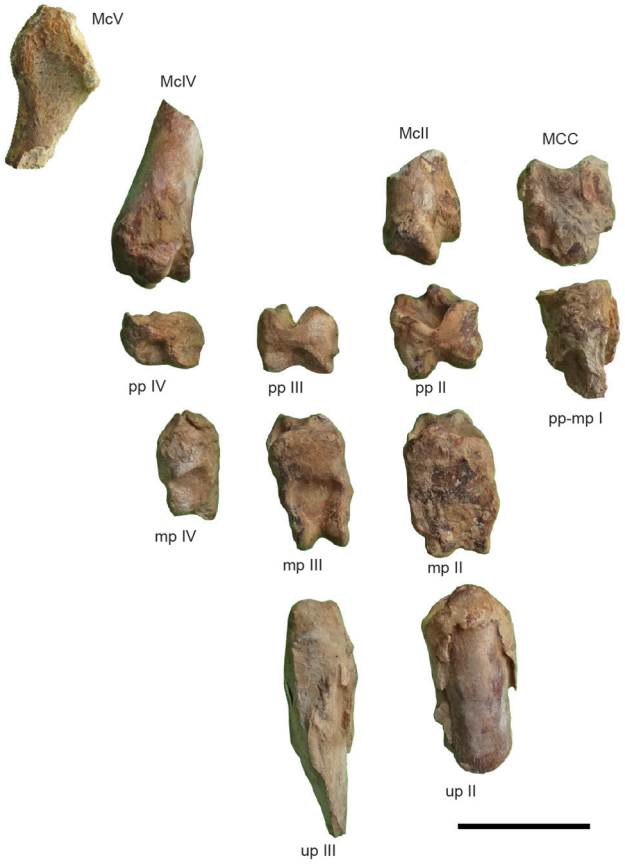

Figure 8. ***Thalassocnus carolomartini*** **(SGO.PV** 15500) from the Lomas del Sauce locality. Partial digit complex of the right manus in dorsal view. Abbreviations: **m,** middle phalanx; **Mc,** metacarpal; **MCC,** trapezium-first metacarpal complex; **pp,** proximal phalanx; **up,** ungueal phalanx. Scale bar= 5 cm.

socnus are presumably fused (Amson *et al.*, 2015b). The fused phalanx in the Lomas del Sauce specimen is incomplete, lacking the distal end, so no observations related to the curvature of these bones could be made. The proximal articular facet in the Lomas del Sauce proximal phalanx is oval and concave, similar to that of *T. littoralis* and *T. carolomartini* (no data for *T. yaucensis*) but different in its dorsal extension (Amson *et al.*, 2015b). Whereas in *T. littoralis* and *T. carolomartini* this facet almost covers the entire proximal end of the bone, in the Lomas del Sauce digit, it does not reach the dorsal edge and occupies just three-quarters of the dorsopalmar depth of the bone.

The Lomas del Sauce specimen preserves only the distal end of the second metacarpal and, therefore, diagnostic measurements of PD length and DP depth in the midshaft could not be made. In *Thalassocnus*, the distal carina for the articulation with digit two is large and well developed. It is broadly curved dorsopalmarly and less so mediolaterally. The carina morphology indicates that digit two was rotated, with its morphologically palmar side facing medially. This torsion can be measured by determining the angle between the vertical plane and the distal carina. This angle is greater in the younger species. The Lomas del Sauce second metacarpal presents an angle of 36°, similar to that of *T. carolomartini* and *T. yaucensis* (Amson *et al.*, 2015b), whose values are between 35-40°.

Digit two is complete in the specimen from Lomas del Sauce. Some characters of the middle and ungual phalanges are diagnostic. In *Thalassocnus*, the distal articular surface of the middle phalanx (for the ungual phalanx) forms a trochlea with an almost circular shape in lateral and medial views (Amson *et al.*, 2015b). The lateral condyle is slightly larger than the medial one. In *T. antiquus* and *T. littoralis* (no data for *T. natans*), the lateral condyle only protrudes dorsally from the level of the dorsal edge of the medial condyle while in *T. carolomartini* and *T. yaucensis*, the lateral condyle protrudes dorsally and palmarly. The Lomas del Sauce specimen presents the characteristics of the two youngest species. Moreover, during maximum flexion, the angle formed by the long axes of middle and ungual phalanges reaches 61° in the Lomas del Sauce specimen and is similar to the values measured for *T. carolomartini* and *T. yaucensis* (Amson *et al.*, 2015b).

The complete digit three is preserved in the Lomas del Sauce specimen, with free proximal and middle phalanges. In this feature, it resembles *T. carolomartini* or *T. yaucensis*, whereas in the older species these two phalanges are co-ossified.

The proximal and distal ends of the fourth metacarpal are preserved in the Lomas del Sauce specimen. *T. littoralis* and *T. carolomartini* possess a fossa at the junction of the facets for the unciform and the third metacarpal, which is smaller in the former species. *T. natans* and *T. yaucensis* lack this fossa. In the Lomas del Sauce specimen, this fossa is absent. The flat morphology of the articular surface for the fifth metacarpal fits with that described of *T. carolomartini* or *T. yaucensis*, departing from the concave surface found in the older species.

The pelvis is partially preserved, including a nearly complete right and partial left ilium as well as the anterior portion of the sacral vertebrae (Fig. 9). Furthermore, the anterior and lateral edges of the sacroischiatic foramen and the anterior part of the right acetabulum are preserved. The dorsal surface of the ilium presents a markedly raised edge from the level of the third sacral vertebra on its medial side to the midpoint of the anterior edge. The delimitated area, lateral to this ridge, bears a shallow concavity. An iliopectineal eminence located just anterior to the acetabulum, on the lateral edge of the right ilium, is found in *T. antiquus*, *T. littoralis*, and *T. carolomartini* [no data for the other species; Amson *et al.* (2015c)] but not in the Lomas del Sauce specimen.

Partial left and right femora are preserved in the Lomas del Sauce specimen of *Thalassocnus* (Figs. 10–11). As described in Amson *et al.* (2015c), there is a sharp narrow crest extending proximally from each epicondyle on the edge of the diaphysis. In the posterior side of each crest, there is a fossa just proximal to each condyle. The medial crest forms a very fine lamina in *T. natans* and *T. littoralis* but is more robust in *T. carolomartini* (no data for *T. yaucensis*), as it is in the Lomas del Sauce specimen. Moreover, the patellar surface of the Lomas del Sauce specimen is symmetrical, with the lateral and medial trochlear ridges reaching almost the same anterior level in distal view (Fig. 10.4). This is one of the diagnostic characters of *T. carolomartini* and *T. yaucensis*. In order to compare this trait in the different species, the anteroposterior depth of the medial trochlear ridge, located anterior to the level of the lateral trochlear ridge (MTR), and the depth of the distal epiphysis at the level

Figure 9. ***Thalassocnus carolomartini*** **(SGO.PV** 15500) from the Lomas del Sauce locality. Pelvis in dorsal view. Fragments on the right side are parts of the iliac wing originally broken *in situ* just before or during burial. Scale bar= 5 cm.

of the lateral trochlear ridge (LTR) (Amson *et al.*, 2015c) were measured. A ratio between the two values was then calculated. *Thalassocnus* shows a progressive decrease in the values of this ratio from the oldest to the youngest species. Values obtained for the Lomas del Sauce specimen are even lower than those measured in *T. yaucensis* (Fig. 10). Another feature that the Lomas del Sauce specimen has in common with one of the youngest species is the similar distal extension reached by both condyles in anterior view (Fig. 10.2).

Both the left and the right patellae are preserved in the Lomas del Sauce specimen of *Thalassocnus* (Fig. 12). The patella has a teardrop shape in anterior and posterior view due to the progressive tapering of the apex distally. In the Lomas del Sauce specimen, the apex is not bent posteriorly as it is in all species of *Thalassocnus* except *T. antiquus*. In *Thalassocnus*, the articular surface for the femur is convex mediolaterally in correlation with the patellar surface of the femur. The surface on the patella is divided into two parts, one medial and one lateral, both of which present a shallow concavity proximodistally. In the Lomas del Sauce specimen, the lateral surface is wider mediolaterally and larger proximodistally than the medial one. This is consistent with the morphology present in the youngest species of *Thalassocnus* (no data for *T. carolomartini*). The older species feature a wider medial surface (Amson *et al.*, 2015c).

Both the right and the left proximal ends and the left distal end of the tibiae are preserved in the Lomas del Sauce specimen (Figs. 13–14). The medial condyle of the proximal epiphysis is oval, unlike that of *T. antiquus,* in which this facet is more circular (Amson *et al.*, 2015c). The articular surface for the astragalus is formed by two concavities separated by a median ridge along the entire anteroposterior depth of the distal surface. This is also the condition in all *Thalassocnus* species except *T. yaucensis*, in which the ridge does not reach the posterior side of the epiphysis. In the Lomas del Sauce specimen, the central ridge is continuous to the elevated posterior edge of the distal tibia.

The complete left fibula and the proximal end of the right one are preserved (Fig. 15) in the Lomas del Sauce specimen. The articular surface for the tibia is well preserved on the proximal end of the right fibula. As in *T. carolomartini* and *T. yaucensis*, this facet faces proximally and medially (Amson *et al.*, 2015c). Moreover, there is a shallow fossa

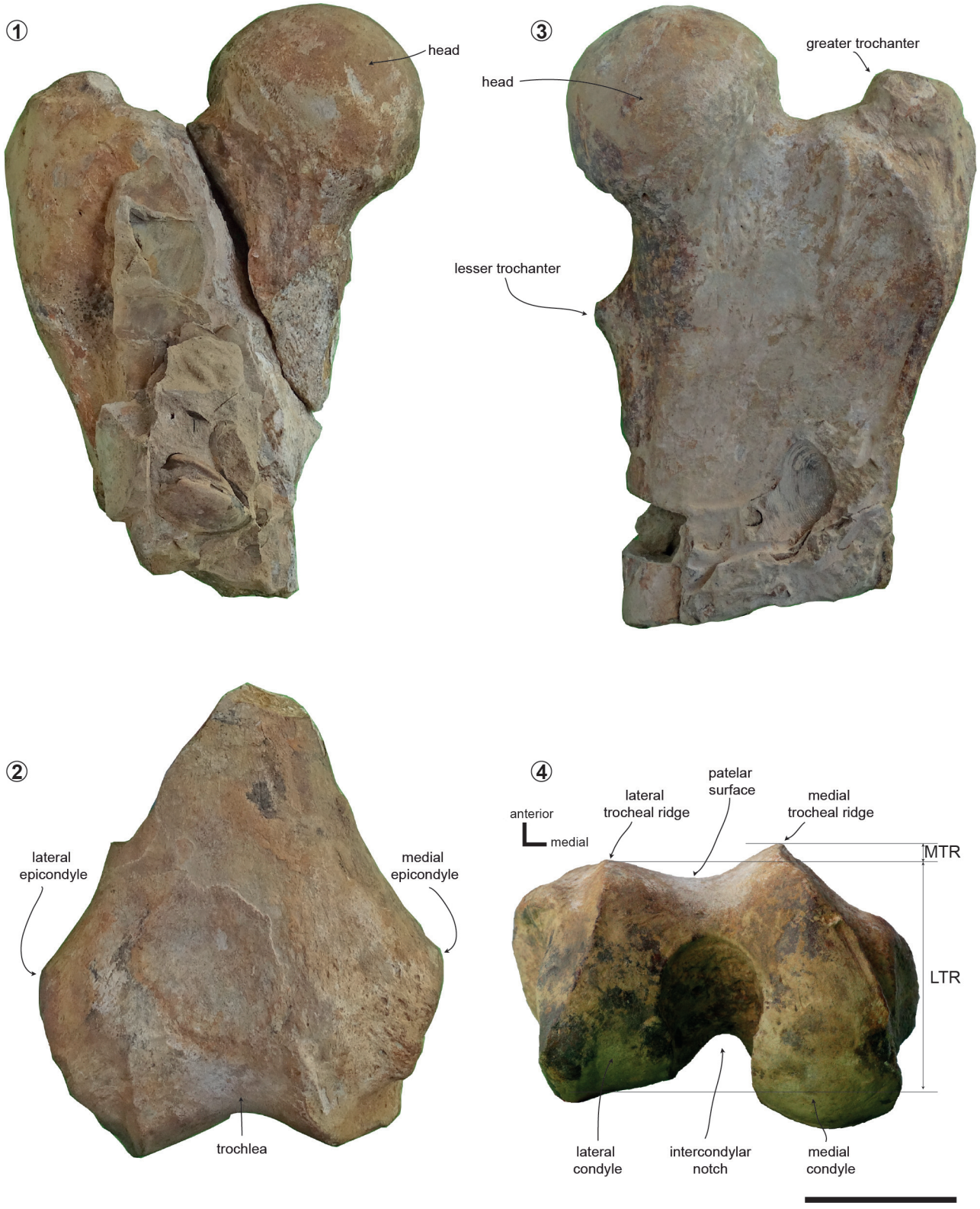

Figure 10. ***Thalassocnus carolomartini*** (**SGO.PV** 15500) from the Lomas del Sauce locality. **1,** right proximal femur in anterior view; **2**, right distal femur in anterior view; **3,** left proximal femur in anterior view; **4**, right femur in distal view. Abbreviations: **LTR,** depth of the distal epiphysis at the level of the lateral trochlear ridge; **MTR,** anteroposterior depth of medial trochlear ridge measured from the level of the lateral trochlear ridge. Scale bar= 5 cm.

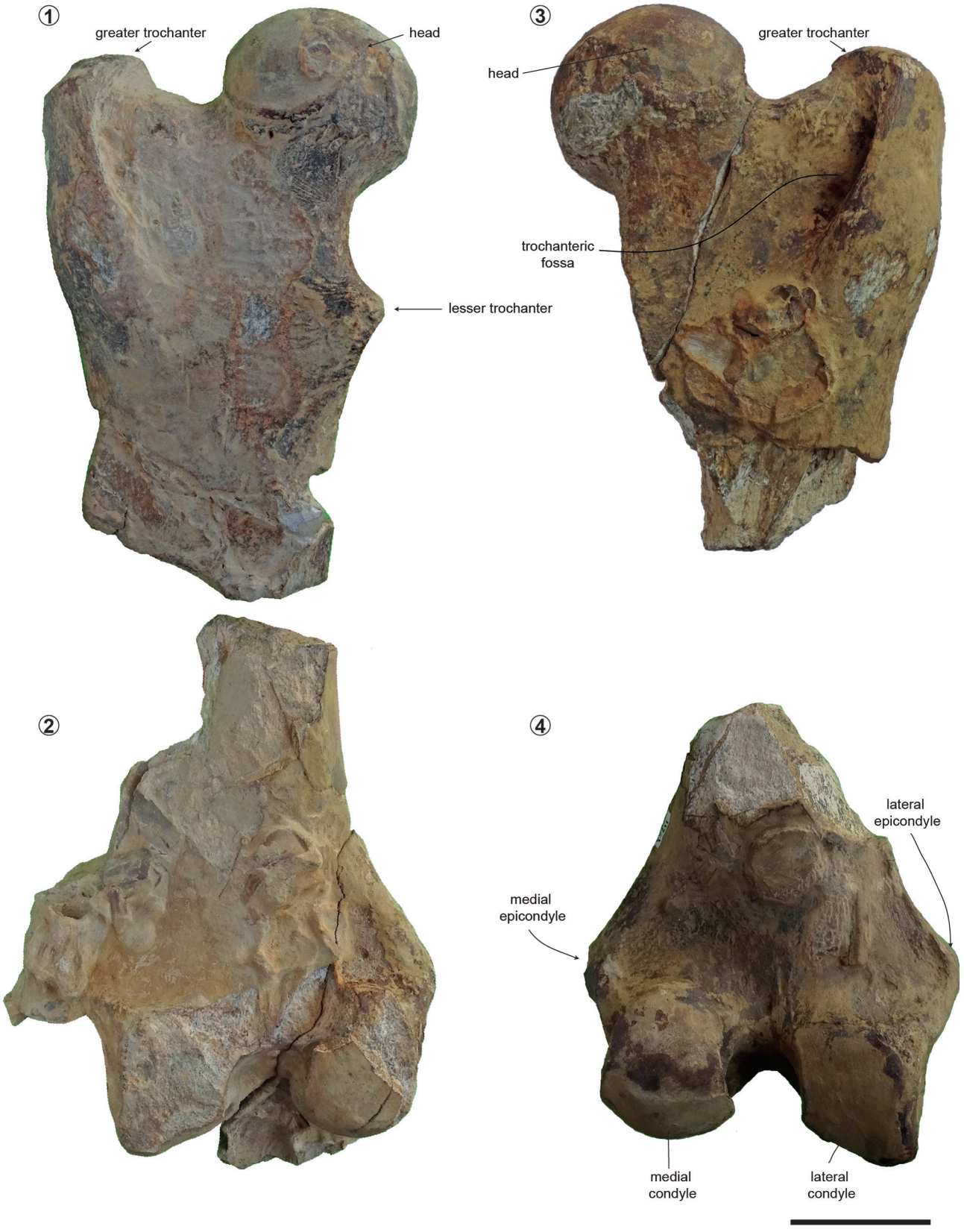

Figure 11. ***Thalassocnus carolomartini*** **(SGO.PV** 15500) from the Lomas del Sauce locality. **1,** left proximal and **2,** left distal femur is posterior view; **3,** right proximal and **4,** right distal femur in posterior view. Scale bar= 5 cm.

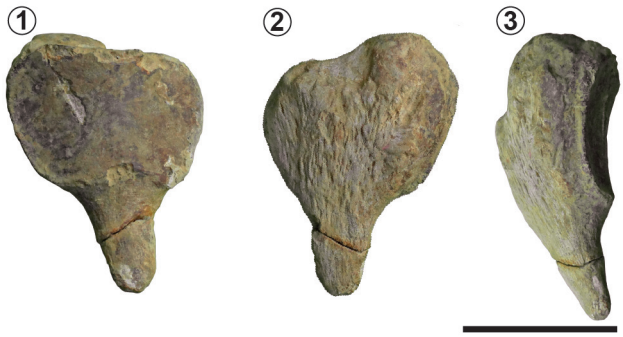

Figure 12. ***Thalassocnus carolomartini*** **(SGO.PV** 15500) from the Lomas del Sauce locality. Left patella in: **1,** posterior view; **2,** anterior view; **3,** lateral view. Scale bar= 5 cm.

distal to this facet in the Lomas del Sauce specimen, similar to that described for the youngest species of *Thalassocnus*. The shaft of the left fibula presents some features that differ from the general description of the genus given by Amson *et al.* (2015c). The Lomas del Sauce specimen has a straight shaft elliptic in cross-section at the midshaft and distal end but teardrop-shaped at the proximal end. The shaft does not have the anterior ridge previously described by Amson *et al.* (2015c). The medial orientation of the tibial articular surface at the distal end of the fibula resembles that of *T. carolomartini* and *T. yaucensis* (Amson *et al.*, 2015c).

The complete right astragalus is preserved (Fig. 16). The

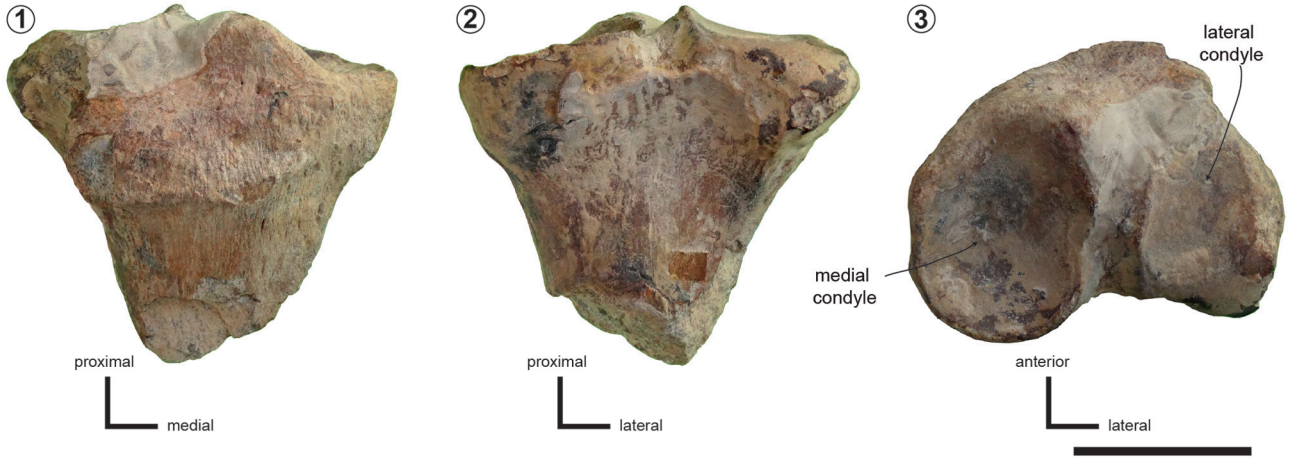

Figure 13. ***Thalassocnus carolomartini*** **(SGO.PV** 15500) from the Lomas del Sauce locality. Proximal end of the right tibia in: **1,** anterior view; **2,** posterior view; **3,** proximal view. Scale bar= 5 cm.

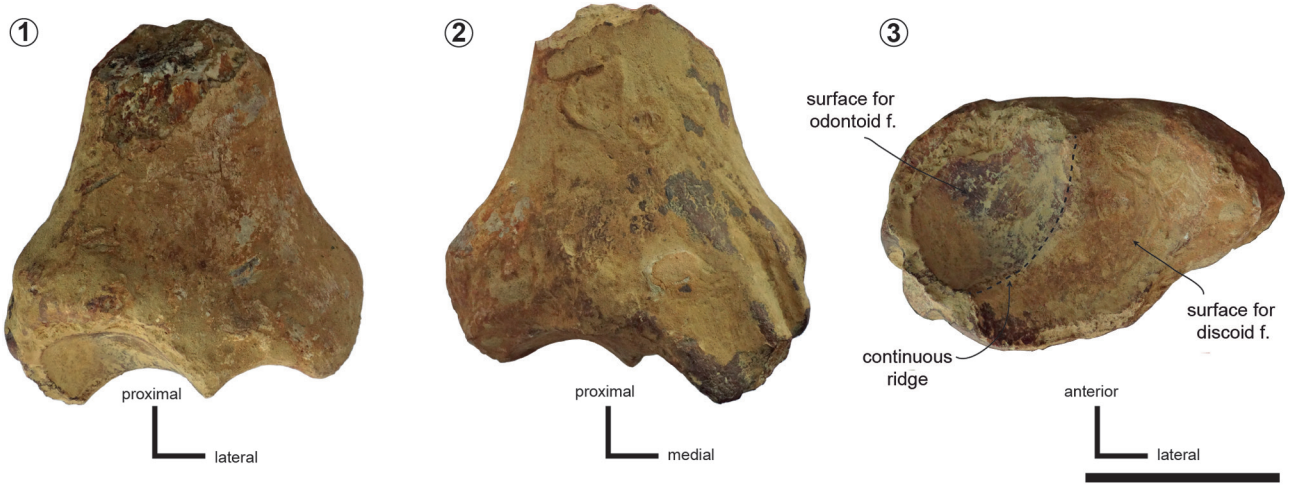

Figure 14. ***Thalassocnus carolomartini*** **(SGO.PV** 15500) from the Lomas del Sauce locality. Distal end of the left tibia in: **1,** anterior view; **2,** posterior view; **3,** distal view. Abbreviation: **f,** facet. Scale bar= 5 cm.

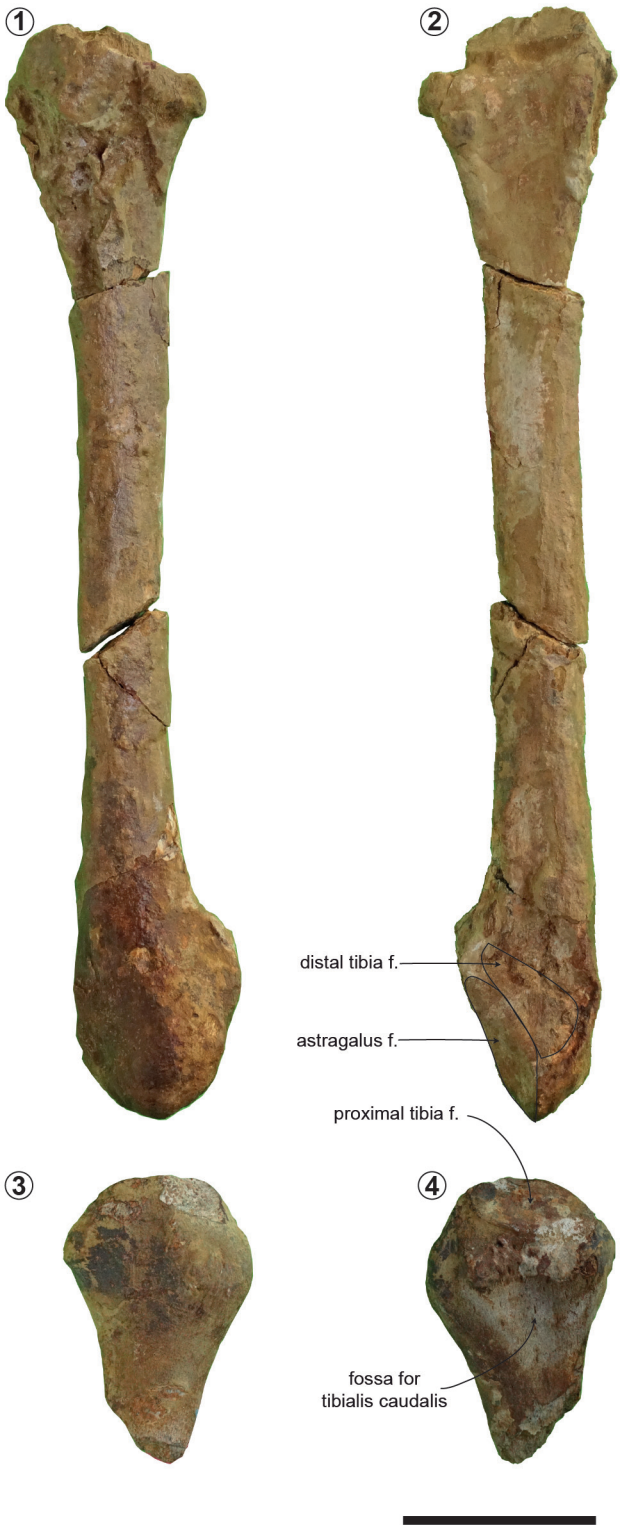

Figure 15. ***Thalassocnus carolomartini*** **(SGO.PV** 15500) from the Lomas del Sauce locality. Complete left fibula in: **1,** lateral view; **2,** medial view; Proximal end of right fibula in: **3**, lateral view; **4,** medial view. Abbreviation: **f,** facet. Scale bar= 5 cm.

distal navicular facet is concave, as in all pilosans, although this concavity is not too marked, a characteristic of the youngest species of *Thalassocnus*. In distal view, the angle between the medial and the lateral trochleae is 109°. This value approaches that of *T. carolomartini*. In the older species, this angle is smaller and, in *T. yaucensis*, it reaches 135° (Amson *et al.*, 2015c). In the Lomas del Sauce specimen, as in all species of *Thalassocnus* except *T. yaucensis*, the angle between the odontoid and the discoid facets is well defined along the whole proximodistal length of the astragalus.

The left cuboid is preserved in the Lomas del Sauce specimen (Fig. 17). In *T. natans* and *T. antiquus*, the distal edge of the articular surface with the fourth metatarsal is marked by a median notch that is reduced or almost absent in the younger species. In the Lomas del Sauce specimen, this notch is absent.

The complete and articulated cervical (atlas, axis and third to seventh cervical vertebrae) and some thoracic vertebrae (first to ninth thoracic vertebrae) as well as fragmentary disarticulated thoracolumbar vertebrae are preserved in the Lomas del Sauce specimen. Five isolated caudal vertebrae were also recovered. In *Thalassocnus*, a progressive acquisition of cranioventral inclination of the cranial articular facets of the atlas is found. This inclination increases from the older to the younger species (Amson *et al.*, 2015d). The angle formed by the cranial facets and the horizontal axis reaches 20° in *T. yaucensis*, making the cranial facets visible in ventral view (no data for *T. carolomartini*). A similar morphology is observed in the Lomas del Sauce specimen. The caudal inclination of the thoracic spinous processes also distinguishes the different species of *Thalassocnus*, as it increases from the older to the younger species. The angle between the cranial edge of the spinous process and the dorsoventral axis on the T2 vertebra is of 30° in *T. antiquus* and *T. natans*, and around 40° for the younger species. This angle increases caudally up to T9 (Amson *et al.*, 2015d). In the Lomas del Sauce specimen, the spinous process angle was of 45° at the T3 vertebra.

The ribs preserved in the Lomas del Sauce specimen are fragmentary. Although histomorphometric measurements were not performed, broken surfaces revealed a very compact inner structure reminiscent of the youngest species of *Thalassocnus* (Amson *et al.*, 2015a, d).

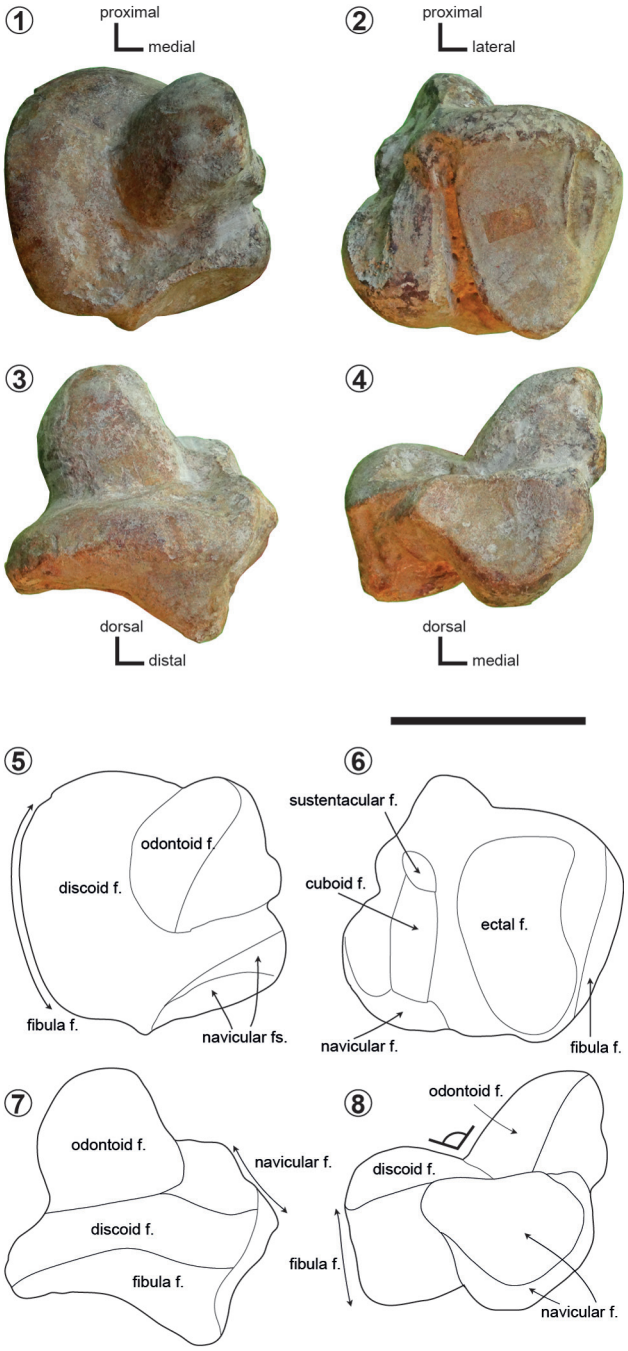

Figure 16. ***Thalassocnus carolomartini*** (**SGO.PV** 15500) from the Lomas del Sauce locality. Right astragalus in: **1, 5,** dorsal view; **2, 6,** plantar view; **3, 7,** lateral view; **4, 8,** distal view. Abbreviation: **f,** facet. Scale bar= 5 cm.

***Thalassocnus littoralis*?, *carolomartini*?, *yaucensis*?**

Figure 18

Referred specimen. SGO.PV 21545, isolated right coossified proximal and middle phalanges of the third digit of the pes.

Locality and age. Playa la Luna locality, Chile; Horcón Formation, Pliocene.

Description. Just proximal to the condyles, the plantar fossa is deep, as in *T. littoralis*, *T. carolomartini* and *T. yaucensis* (Amson *et al.*, 2015c). Its proximodistal length (at mid width; *ca.* 31 mm) falls within the range of those species as well.

DISCUSSION AND CONCLUSIONS

The morphological features described for the Lomas del Sauce specimen and related to diagnostic features in the forelimb, the hind limb, and the axial postcranium enable us to safely attribute this specimen to either *T. carolomartini* or *T. yaucensis*. However, discriminating between the two species is somewhat difficult because they share many morphological features postcranially and are distinguished primarily based on the cranium (Amson *et al.*, 2015a–d).

Regarding the forelimb, the symmetry of the distal end of the humerus and the morphology of the proximal end of the ulna suggest an attribution to *T. carolomartini*. However, the morphology of the trapezoid articular surface on the scaphoid of the Lomas del Sauce specimen fits with that of *T. yaucensis*. The relative width of the scaphoid, which increases from the oldest to the youngest *Thalassocnus* species, is intermediate between the values previously reported for *T. carolomartini* and *T. yaucensis* (Amson *et al.*, 2015b).

With respect to the hind limb, the most important features distinguishing *T. carolomartini* from *T. yaucensis* relate to the distal end of the femur, the astragalus and the corresponding articular surface in the distal end of the tibia (Amson *et al.*, 2015c). The distal end of the femur in distal view is increasingly symmetrical from the oldest to the youngest species of *Thalassocnus* due to the reduction of the medial trochlear ridge. In the Lomas del Sauce specimen, the development of this ridge is most reminiscent to that of *T. yaucensis* (Amson *et al.*, 2015c). In the astragalus of the Lomas del Sauce specimen, the morphology of the odontoid and the discoid trochleae, including the angle formed by these two facets, is consistent with an attribution to *T. carolomartini*. No diagnostic features enabling the discrimination between *T. carolomartini* and *T. yaucensis* were found in the cervical and thoracic vertebrae of the Lomas del Sauce specimen.

Most diagnostic features suggest an attribution of the

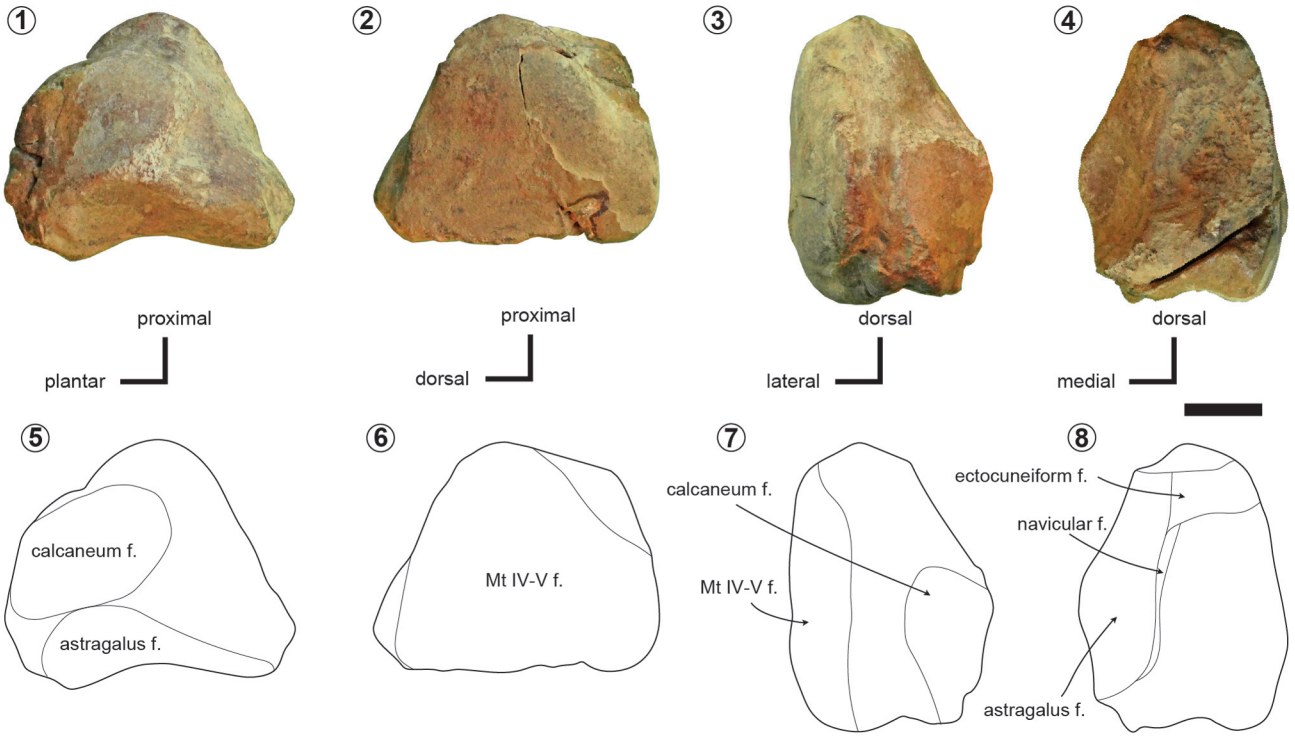

Figure 17. ***Thalassocnus carolomartini*** **(SGO.PV** 15500) from the Lomas del Sauce locality. Left cuboid in: **1, 5,** medial view; **2, 6,** lateral view; **3, 7,** proximal view; **4, 8,** distal view. Abbreviation: **f,** facet; **Mt,** metatarsal. Scale bar= 1 cm.

Lomas del Sauce specimen to *T. carolomartini*. The finding of a few features that are more reminiscent of *T. yaucensis* (*e.g.*, the shape of the facet for the trapezoid on scaphoid, the width of the scaphoid and the shape of the femoral trochlea) might suggest that these features are in fact also characteristic of *T. carolomartini*. In other words, an amendment of the description of the younger species may be required. It might also be that the Lomas del Sauce specimen presents an overall morphotype that is an intermediate between those previously described for *T. carolomartini* and *T. yaucensis*. For the sake of simplicity, we prefer to ascribe the Lomas del Sauce specimen to *T. carolomartini*.

In light of the morphology of the plantar fossa and of the overall length of the specimen, the isolated phalanx of *Thalassocnus*, found in the Horcón Formation, may be attributed to one of the species of *Thalassocnus* younger than *T. natans*.

As only *T. antiquus* or *T. natans* were previously reported in Chile (Canto *et al.*, 2008; Pyenson *et al.*, 2014), the Lomas del Sauce specimen represents the first occurrence of the younger species *T. carolomartini* outside the Peruvian Pisco

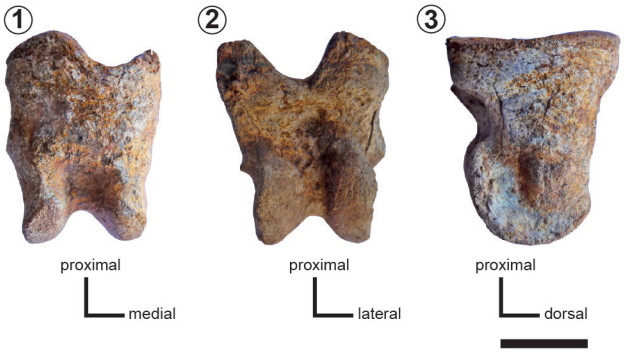

Figure 18. ***Thalassocnus littoralis***?, ***carolomartini***?, ***yaucensis***? **(SGO.PV** 21545) from the Playa la Luna locality. Coossified proximal and middle phalanges of the digit three of the right pes in: **1,** dorsal view; **2,** palmar view; **3,** lateral view. Scale bar= 2 cm.

Formation. Furthermore, the Lomas del Sauce (Coquimbo Formation) and Playa la Luna (Horcón Formation) localities are situated at higher latitudes than those of all the previously reported occurrences of *Thalassocnus*, therefore extending the geographic range of the genus by more than 5° of latitude.

Such extension of the geographic range for *Thalassocnus* raises the question of the coastal paleoenvironment of the Pacific coast of central Chile during the Pliocene. It was hypothesized that the younger species of *Thalassocnus* grazed on marine vegetation, most likely seagrasses (Muizon *et al.*, 2004b; Amson *et al.*, 2015d). Currently, seagrasses are largely restricted to tropical and subtropical areas, so it is important to note that today they are only known along the modern Pacific coast of South America by a small meadow in the Coquimbo district (Kuo, 2005) of coastal Chile, a patch most likely insufficient to sustain a population of large marine grazers. It has been hypothesized that this meadow is a relict population and that seagrasses were formerly more widespread in Chile (Phillips *et al.*, 1983). Like sirenians (Vélez-Juarbe, 2014), the fossil record of *Thalassocnus* could be a proxy for seagrass paleodistribution. Thanks to the specimens from the Coquimbo and Horcón formations reported here, it can be concluded that *Thalassocnus* was found ranging from at least ca. 14°S to 32°4'S. This corroborates the hypothesis of Phillips *et al.* (1983), which can even be extended, because populations of seagrasses developed enough to sustain large marine grazers were most likely present at least during the Pliocene in the whole central region of the Pacific coast of South America.

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